

Chapter 16

Apomixis as a Facilitator of Range Expansion and Diversification in Plants

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Abstract Apomixis, the asexual reproduction via seed, often occurs in huge plant polyploid complexes with large geographical distributions. However, the long-term evolutionary fate of asexuals traditionally was regarded as doomed by extinction. A seven-step evolutionary model is presented to explain the role of sex → apomixis shifts on geographical cytotype distributions, and the potential consequences of reversals apomixis → sex on plant diversity. Accordingly, apomictic polyploid genotypes act as facilitators for range expansions of asexual taxa in agamic complexes by functioning as pioneer explorers of new niches. High intragenomic (allelic) diversity and epigenetic variability may help for rapid adaptation. Therefore, they could rapidly expand the distribution areas of their progenitor sexual populations by occupying new ecological niches and geographical areas. Hence, apomixis would result in divergent patterns of geographic distribution between sexual and asexuals, a pattern described as “geographical parthenogenesis,” in which apomicts occupy extensive geographical areas and higher latitudinal zones while sexual relatives are restricted to small refuges. Later on, reversals to complete sexuality would allow for the establishment of new sexual populations in different habitats without the long-term disadvantages of asexuality. The new sexual recombinants will be genetically isolated from the original sexual populations and consequently predisposed to a divergent evolution, and potentially enabled to evolve into new sexual species. The present model stresses a previously unidentified evolutionary significance of the geographical parthenogenesis as a motor for plant diversification.

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16.1 Introduction

Angiosperms are the most successful group of the plant kingdom. Features such as hybridisation and polyploidy are major contributors to evolution and diversification in angiospermous lineages (Soltis and Soltis 2009; Jiao et al. 2011), often connected to shifts between sexuality and asexuality (Asker and Jerling 1992). On the other hand, asexuality in angiosperms has long been seen as a reproductive strategy that rather restricts evolution by limiting genetic reshuffling (Stebbins 1950).

Asexual taxa are characterized by the lack or malfunctioning of normal mechanisms enhancing variability in natural populations (i.e., meiotic, chromosomal, and gametic recombination). Traditional views regarded apomixis as a blind alley of evolution (Darlington 1939) because of the lack of variation and hence reduced adaptive potentials. (Stebbins 1950) noted that apomictic complexes harbour just variation on the same theme, and that apomicts failed to evolve new genera.

Here, we present an alternative view of apomixis (i.e., the asexual reproduction via seeds = agamospermy) as promoter of diversification and evolution. Present geographical distributions of apomictic complexes rather suggest broad range expansions and altogether broad ecological niches compared to sexual relatives (Kearney 2005, Hörandl 2006). This phenomenon termed “geographical parthenogenesis” was so far regarded just a short-term success of sexuality (Van Dijk 2003), and most explanations relate the causality to short-term ecological differentiation. This view probably neglects the dynamics that is inherent in agamic polyploid complexes. Research of the last decades suggests that the dynamics in origin, genetic, and developmental features within agamic complexes has been strongly underestimated. Here, we will discuss (1) developmental variability enhancing genetic variation, (2) natural origins agamic complexes and dynamics among lineages as sources for genetic variation, (3) intragenomic allelic diversity and epigenetic variation as potential factors for adaptation to environmental heterogeneity, (4) recent findings of geographical patterns and niche differentiation in various model systems, and (5) hypothetical scenarios of reversals from asexuality to sexuality which may open further evolutionary potentials for speciation.

16.2 Asexual Plants as Uniform Clones: A View with Many Scarcities

In this section, we will introduce a simple definition of clone at the organismal level, considering single plants as individuals rather than the “evolutionary individual” in the sense first raised by Janzen (1977), to place our discussion and pinpoint snags surrounding the view of clonality.

A clone is a number of ramets which belong to the same genet (Richards 1997), i.e., a number of physiologically independent individuals with the same genetic constitution (or genotype). Hence, a cloning process must exactly reproduce the

genetic composition of the individual in the absence of genetic recombination. In angiosperms, plants can reproduce asexually and generate “clones” following dissimilar processes. The two most important categories are vegetative propagation and apomixis.

Vegetative propagation involves the formation of new individuals through specialized structures without production of seeds or spores, and hence, meiosis and syngamy are avoided. There are many types of structures to propagate vegetative daughter plants, including plantlets and bulbils (vivipary), stem offshoots or adventitious shoots, rhizomes and stolons, runners, bulbs, and tubers. Dispersal capacities of each of these propagation strategies are variable and can be limited to a small area usually close to the mother plant or big extensions, occupied by one or few clones (e.g., the invasive Canadian pondweed, *Elodea canadensis* Michx.; Gustafsson 1946).

Apomixis includes many different developmental patterns, clustered in three general groups, i.e., diplospory, apospory, and adventitious embryony (Asker and Jerling 1992). Diplospory starts the development from an unreduced megaspore, while in apospory, a somatic cell takes over a megaspore-like cell fate; in both cases, an unreduced egg cell is formed which develops parthenogenetically. Adventitious embryony involves the direct development of embryos out of somatic cells. All three general patterns involve the formation of new individuals through seeds, although meiosis and syngamy might be partially or completely avoided. Consequently, apomictic plants take the advantage of producing dispersal units (diaspores) with higher dispersal capacity compared to vegetative propagation strategies. Most important, apomictic development of embryos starts from a single-cell stage, either an unfertilized egg cell or a somatic cell, while vegetative development starts from multicellular tissues (Mogie 1992).

Although clones are expected to be genetically uniform, because of several reasons, 100 % pure clones rarely exist in nature (Avisé 2008). Individual plants are formed by thousands, even millions of mitotically derived cells. Even though DNA repair mechanisms inside cells are efficient, they are not perfect. A few *de novo* mutations will arise in a genome during DNA replication and will be retained during the plant development. While in vegetative propagated plants, meristems are multicellular and hence mutations produce chimeric tissues, apomictic plants goes through a single-cell stage that increases on the one hand the chance of the elimination of deleterious mutations as all daughter cells will inherit this mutation (Grosberg and Strathman 2007) and on the other hand the chances of establishment of distinct genotypes carrying particular adaptive mutations (Van Dijk et al. 2009). Moreover, another three processes can slightly reduce the 100 % genetic identity expected among clonemates (Avisé 2008). The first one is gene conversion, a process in which recombination between members of the same gene family (e.g., duplicated genes) occurs at ectopic places (nonallelic or paralogous recombination) involving unidirectional exchange of DNA sequences (e.g., Datta et al. 1997). In angiosperm genomes, there is an appreciable rate of gene conversion between genes duplicated during ancient polyploidization events (i.e., paleologous genes) (Wang and Paterson 2011).

The second process is mitotic recombination, an atypical crossover event between homologous chromosome segments that can occur during repair of spontaneous DNA damage (Andersen and Sekelsky 2010). However, as pointed out by Gorelick (2014), although mitotic recombination in the sense of crossing over events per cell division occurs at much lower rates than normal meiotic recombination (Pontecorvo and Käfer 1958; Andersen and Sekelsky 2010), a single individual plant undergoes a lot more mitotic than meiotic cell divisions, especially in large clonal plants. The third process showing increasing relevance on studies of clonality is what Martin (2005) described as “epigenetic drift.” Epigenetic drift refers to the differential acquisition of epigenetic marks in organisms with the same genetic constitution and, naturally, affected by different or even slightly different environmental sceneries and ecological interactions. Thus, epigenetic variation acquired in long-lived asexual organisms may critically influence genotype development and plasticity by differential gene regulation, creating genetic differences among clonemates (e.g., Verhoeven and Preite 2013; Douhovnikoff and Dodd 2015). The age and growth rates of each particular genet/genotype will influence on the relative impact of those gene-based processes on clones’ genetic composition. Depending on particular cases, the longevity of clonal plants can vary between few and several thousand years (de Witte and Stöcklin 2010). Henceforth, *de novo* mutations, gene conversion, mitotic recombination, and epigenetic drift processes may certainly work as an important source of genetic and genomic variation which would make the assumption of genetic uniformity of large and long-standing clones in nature something hardly ever valid.

An extra decisive point unconnected to the last-mentioned gene-based processes that occur only in apomictic plants is that they usually are not obligate apomicts in the sense that the normal meiotic pathway still can be functional (Asker and Jerling 1992). Therefore, most apomicts produce low levels of sexually derived individuals together with the clonally derived ones. Consequently, natural populations of apomicts show greater genotype variability compared to that expected from a clone. Although levels of functional sexuality are generally low, they show a large range of variation depending upon genotypic, environmental, and ecological conditions (e.g., Aliyu et al. 2010; Bicknell et al. 2003; Cosendai et al. 2011; Hojsgaard et al. 2008, 2013, 2014b; Majeský 2013; Noyes and Givens 2013; Quarin 1986; Rebozzio et al. 2011, and have clear consequences on asexual genome evolution, e.g. buffering Müller’s ratchet effect of mutation accumulation expected in strictly asexual organisms (Müller 1964; Hojsgaard and Hörandl 2015). Hence, the proportion of recombinant seeds and individuals will be different for each particular genetic system and probably for each area and time of the season considered. Anyhow, if meiosis can still be functional, there will be high probabilities of injecting new recombinant genotypes in any apomictic population. Whether such genotypes will be successful and establish a new lineage in a particular situation would depend upon different factors. Such factors may include internal causes (developmental and genetical or genomic related; e.g., Hojsgaard et al. 2013; Pellino et al. 2013; Hojsgaard and Hörandl (2015) or external ones (competition against other genotypes, niche shifts, etc.; e.g., Pearman et al. 2007).

16.3 Apomixis and the Formation of Agamic Complexes

Diploid plants are the primary source of new polyploids (Ramsey and Schemske 1998). Multiple origins of polyploids from different hybridization events between diploid parental species results in various polyploid derivatives, which can also interact with each other (Koch et al. 2003; Guo et al. 2004; Hörandl et al. 2009; Lo et al. 2010, Sochor et al. 2015 among others). Polyploids arisen in a diploid population can also backcross with their parental species in different ways and will have diverse outcomes. The interaction between such derivative polyploids and their ancestral diploids form polyploid complexes that reshape many aspects of the species variability (morphologically, physiologically, cytogenetically, ecologically, genetically, etc.). Babcock and Stebbins (1938, pp. 55–56) defined a polyploid complex as:

a group of species, containing forms with different chromosome numbers, of which those with the lowest number (i.e., the diploids) are more or less distinct from one another morphologically, and are usually isolated from one another by sterility barriers, but in which some of the (aneuploid or) polyploid type(s) (are) is intermediate between the diploids or show different recombinations of their characteristics.

Since polyploidy in plants may or may not be associated with reproductive shifts, two types of complexes can be found: (1) sexual polyploid complexes, in which only sexual diploid–polyploid associations are observed; and (2) agamic polyploid complexes, in which the normal sexual reproduction in the new polyploids is partially or completely replaced by some kind of asexual propagation for dispersal, e.g., bulbils, nucellar embryony, and gametophytic apomixis (Babcock and Stebbins 1938; Grant 1981). While the first type is the most frequent in plants, the second is less recurrent, connected to the inferior frequency of apomixis in angiosperms (Hojsgaard et al. 2014a). Thus, agamic complexes are shaped by polyploidy, hybridization, and apomixis, three major processes responsible of evolutionary change and the formation of an array or “complex” of microspecies carrying different character combinations (morphological, cytological, and genetic) from parental species and higher ploidy taxa (usually derivatives). The establishment of “microspecies” is the primary result of apomixis, and consequently microspecies connect morphological gaps between the diploid sexual species blurring discontinuities and causing taxonomic difficulties (Babcock and Stebbins 1938; Gustafsson 1947; Stebbins 1950; Grant 1981; Hörandl 1998; Haveman 2013). From an evolutionary point of view, those microspecies represent relatively successful cases of new character combinations, new genotypes, and/or cytotypes produced by introgression of sexual parentals and/or apomicts derivatives in which residual levels of sexuality are still functional. The level of taxonomic complexity is thought to be contingent with the evolutionary stage of development of the agamic complex (see examples in Babcock and Stebbins 1938; Gustafsson 1947; Grant 1981). Thus, a “young” complex will be considered that one in which parental sexual species together with few microspecies occur in nature and show restricted geographical distribution. In the same direction, a “mature” agamic complex would be that one presenting sexual parentals together with a relatively high number of agamospermous microspecies and widely

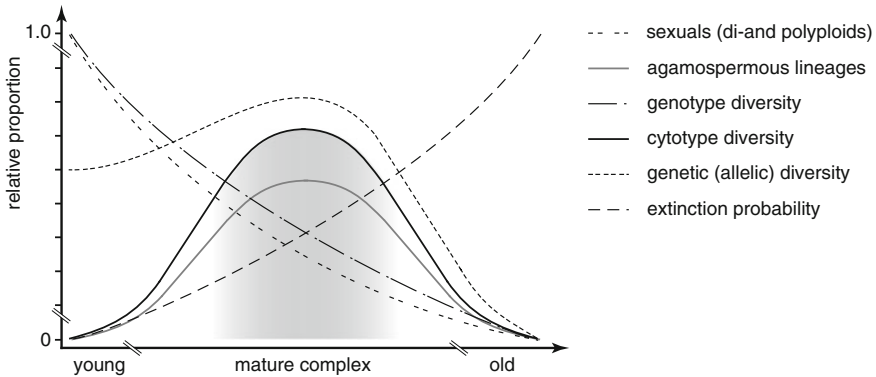
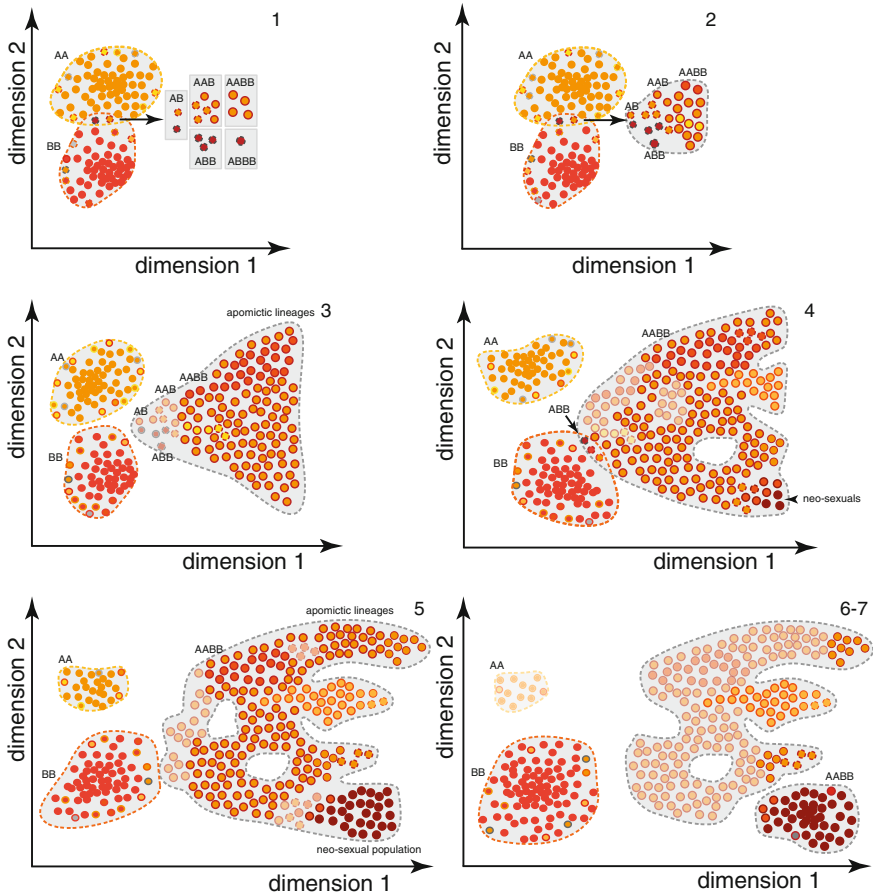


Fig. 16.1 Properties of agamic complexes expected and observed from theoretical models and empirical data after analyses of different successful natural agamic complexes (without considering reversals to sexuality). The abscissa represents a time gradient starting with the origin of the first apomictic lineage. Distribution of values in both axes can vary according to genomic properties and evolutionary flexibility of each particular genetic system. Sexual individuals and/or cytotypes will start to decrease while a proportional increase of asexual lineages. Sexual populations and/or species will decrease following normal extinction rates plus competition with asexual polyploid lineages. Agamosperous lineages will increase by recurrent formation and mutation/recombination processes acting on previously established lineages. Genotype diversity will decrease with elimination of sexual individuals/populations, but will be partially slowed down by the formation of new asexual lineages. Cytotype diversity will increase with the formation of new polyploid and aneuploid lineages mainly via hybridization and polyploidization, but also via partial apomixis (i.e., fertilization of unreduced female gametes), and formation of chromosomally unbalanced gametes. Genetic diversity will be partially maintained or increased during first stages of establishment of the agamic complex by formation of new polyploids that would serve as reservoirs of genetic variability. Finally, the probability of extinction of the agamic complex will increase with the concurrent decrease of sexual individuals/populations, which will drastically influence recurrent formation of new lineages as well as the surviving capacities of established agamosperous lineages along with the other diversity parameters

distributed, while an “old” one would have no extant sexual parents and few surviving agamosperous microspecies (Grant 1981). In natural populations, the sympatric occurrence of sexual (frequently, but not exclusively) diploids associated with apomictic (almost always) polyploids is not uncommon, but in each case, the evolutionary developmental stage should be considered according to particular features of individual complexes. Figure 16.1 represents a summary of theoretical and empirical features expected and observed in different natural agamic complexes (Babcock and Stebbins 1938; Stebbins 1950; Grant 1981). Although initially agamic complexes were seen more as a “closed system” whose final doom depends upon its sexual members (Babcock and Stebbins 1938, p. 61; Stebbins 1950, p. 417), today’s view of agamic complexes has changed. Following Carman’s hypothesis (Carman 1997), apomixis in angiosperms is a result of asynchronous expression of duplicate genes. This hypothesis had found support on different research areas (i.e., embryology, cytology, and gene expression) (e.g., Grimanelli et al. 2003; Polegri et al. 2010; Sharbel et al. 2010; Hojsgaard et al. 2013, 2014b). Under this view, in natural

agamic complexes, apomixis would function as a reproductively stable transitional stage that promotes the evolution of asexual neo-polyploids into regular and developmentally novel sexual paleopolyploid species by functional elimination of gene duplications responsible for apomixis. Therefore, cycles of polyploid agamosperous microspecies formation evolving into new sexually stable species would serve as a facilitator for diversification. The transition-phase hypothesis of Carman (1997) was recently expanded by Hörandl and Hojsgaard (2012) who considered a more dynamic role for new apomictic polyploids within agamic complexes. According to these authors, facultative apomicts with restricted genetic recombination and genotype segregation works as perfect forerunners to explore new eco-geographical areas and niches available only to certain specific genotypes. While sexuality would break down such particular genotypes hampering the access to those areas or niches, facultative apomixis can easily multiply a single genotype without altering gene combinations, whereas it keeps certain level of variation (sexual recombinants). Moreover, although sexual populations theoretically present a cohesive gene pool through a uniform gene flow network among individuals, facultative apomixis allows for the creation of a relatively restricted gene flow network that cracks such uniform gene reservoir within the lineage and isolates populations. With sufficient time, in some areas of widely distributed microspecies, cases of reversal to sexuality could result in a new, and genetically isolated from the parents, sexual population with ample potential to divergent evolution and therefore to maximize species diversification capacities. Following previous features, a model and general outline for the evolution of agamic complexes in nature is drafted (Fig. 16.2).

Even though obligate apomixis was considered as “an escape into a blind alley” with a certain extinction fate (Darlington 1939, p. 113, but also Babcock and Stebbins 1938; Stebbins 1950; Grant 1981), whenever a strict asexual spread into new geographic and ecological areas, it will be subject to new environmental conditions that would promote possibilities for a cytological and genomic re-stabilization of the sexual (meiotic) reproductive program and a complete reversal to sex. The end of the alley may not be strictly a blind one. Based on evolutionary and biogeographical information on apomixis occurrences, Hojsgaard et al. (2014a) found support for the expanded version of Carman’s original hypothesis, as apomixis in angiosperms is highly correlated to those clades with higher levels of diversity (Hojsgaard and Hörandl 2012; Hojsgaard et al. 2014a). Below, we will focus on most important microevolutionary aspects playing a role in different steps of development and evolution of agamic and (when correspond) clonal complexes, as well as their potential role on enhancing plant diversification.



16.4 Apomicts Temporarily Restrict Genetic Variation and Potentiate Plant Ecological Capacities

Apomictic species can found populations via single individuals and are therefore better colonizers than related outcrossers; this colonization ability is most efficient after long distance-dispersal of seeds (Baker's law; Baker 1965). Vegetative propagation, in contrast, remains in terrestrial biota usually spatially restricted. Hence, apomixis combines the benefits of seed dispersal, increasing the potential for long distance-dispersal, and reproductive assurance in the introduced area without the need of pollinators (Hörandl 2006). Even in the case of pseudogamy, self-compatibility enables apomictic plants to use self-pollen for the required endosperm fertilization (Hörandl 2010).

◀ **Fig. 16.2** Hypothetical model for the origin, development, and dynamic of agamic polyploid complexes based on most important microevolutionary processes along a chronological gradient of time (steps). Here, we focus on evolutionary destiny of one single asexual lineage, but many lineages can arise by recurrent formation from sexual parental species through polyploidization and/or hybridization. In the graphics, sexual individuals are represented by uniform colored *circles* (orange and red) and apomictic individuals are shown with different color combinations. Species and lineage distributional areas are included within *dotted lines*. Developmentally and genetically unstable individuals are represented by *dotted circles*. Circle sizes follow individuals' ploidy, and opaqueness identifies ecologically unfitted individuals. 1, a first step would involve a reproductive shift from sexuality to facultative apomixis associated with polyploidization and/or hybridization processes; 2, diversification of apomictic lineages by facultative sexuality, mutation, chromosome re-arrangements, hybridization; 3, range expansions of eco-physiologically fitted genotypes and additional (limited) agamic complex differentiation through mutation and residual sexuality into "cracked" gene pools by gene flow restrictions; 4, occasional re-stabilization of the meiotic reproductive pathway in some lineages (*arrowhead*); 5, complete reversal to sexuality, promoted by niche shift and/or environmental conditions and establishment of a new sexual population (*dark red circles*); 6–7, allopatric speciation of newly formed, biologically and geographically isolated sexual populations (*dark red circles*), and further diversification of genetically cohesive biological species (with the eventual evolution of new genera along time). As expected, each agamic complex is subject to extinction, but when persists, different complexes can be found at different stages of this evolutionary frame. Stages 3–5 may represent mature agamic complexes, while at 6–7 there is a drastic decay of complexity mainly due to ecological changes not alleviated by sexual populations nor asexual lineages which drive them to extinction. Contact zones and introgression with parental species could appear along any of these stages (here is represented in 4). AA, BB: diploid sexual populations/species; AB: diploid hybrids; AAB, ABB: triploid hybrids; AABB: tetraploid hybrids. Dimension 1 and 2 represent any biological, geographical, or ecological gradient outlining the hypothetical distribution, niche and dynamics of populations represented here

However, after colonization, populations have to adapt to novel habitats in the introduced area. Although a "very narrow population niche width" is one of main disadvantages of one agamosperous lineage (Richards 1997), it may not be such in a uniformly patched environment. In a sexual panmictic population, a huge array of genetic variants is expected, each occurring at a certain frequency in space and time. However, a fitted genotype is hardly ever re-created, and such genotype will be lost even when their genes will be uploaded to the population gene pool. Only the population as a whole can adapt to a certain niche. On the contrary, in an agamosperous polyploid complex, broad arrays of individuals derived from few genotypes are being produced, each fitting to a particular niche. Altogether arrays of differentiated clones can fill the total niche space more efficiently than sexual species can do, especially by occupying the extreme niches (Vrijenhoek 1984). This so-called frozen niche variation model was empirically confirmed in many studies (review in Vrijenhoek and Parker 2009; Lo et al. 2013; Mau et al. 2015).

Here, we illustrate how the apomictic genotype can be superior to a sexual population in the same niche space. The same apomictic genotype will be multiplied promoting its spread into the uniformly patched environment. To exemplify this idea, we depict a simple situation where the genotype *Aa* is best adapted to, and hence can disperse on the long term in a relatively uniform ecological niche space (Fig. 16.3). In both sexual and asexual reproductive situations, self-compatibility is

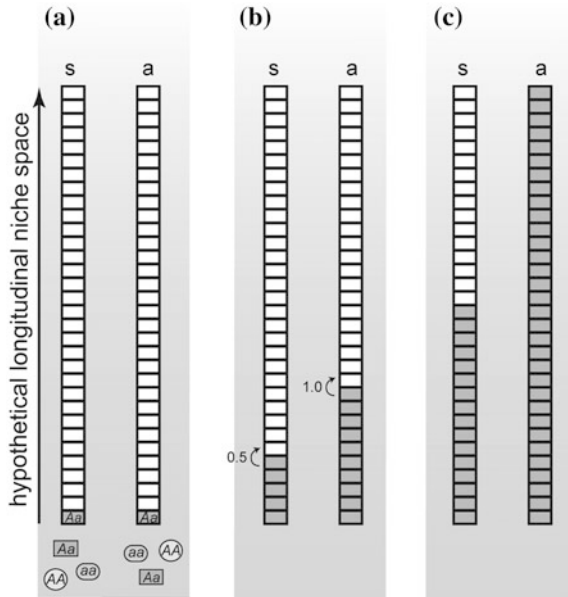


Fig. 16.3 Scheme representing species ecological capacity to occupy a hypothetical patched niche offered (vacant) under two different reproductive strategies and a single dispersal unit (seeds). After first arrival of a single seed from a (distant) population into a free niche patch (**a**), the fitted genotype will be able to produce self-pollinated seeds and conquer one adjacent patch per generation. For the plant species with a sexual strategy, Mendelian chromosome segregation would produce 0.25AA, 0.5Aa, and 0.25aa individuals. Since mainly genotypes Aa can adapt well to specific niche requirements, through sexuality the species can occupy one patch every second generation. For the species with the asexual strategy, apomixis will multiply exclusively the fitted genotype Aa, and hence, one free patch can be conquer every generation. Thus, apomicts will widespread here twice as fast as sexuals (**b**), but when considering genotype complexity and adaptation to a particular heterogeneous niche, the relative occupancy speed gained by producing clonal individuals would be even higher as proportions of fitted genotypes when considering many gene combinations in segregating sexuals will certainly be lower than 0.5. After n generations (**c**), only the species with the asexual strategy occupy the whole niche space. By restricting genetic segregation, apomicts can potentiate ecological capacities of fittest genotypes within particular niches. Individuals fitting dissimilar niche requirements are represented with different shapes and greyscale colors

assumed, seeds are the dispersal units and only one seed can move to the next accessible site or niche patch per generation. From the graphic is possible to visualize the expected consequences the temporal restriction of genetic variation in asexuals can have potentiating and/or stabilizing ecological plant capacities to occupy faster than sexuals and vastly uniform niches independently of the niche size.

The consequences of vegetative propagation on niche space occupancy would be essentially the same only when consecutive niche patches are close enough to allow dispersal of clonal units. Otherwise, sexuality would have an advantage over vegetative propagation as seeds are the most efficient dispersal units.

16.5 Genomic Background of Adaptation to Environmental Heterogeneity

Although asexuality can be advantageous in uniform ecological conditions, natural landscapes are patchy and environmental heterogeneity, both spatial and temporal, is rather the rule (Stewart et al. 2000). Yet, pioneer plants can use different strategies to adapt rapidly to novel and patchy environments. Several studies have reported shifts of ecological niches of pioneer plants from the native to the new conquered area (Early and Sax 2014; Tingley et al. 2014). In general, rapid adaptation can be facilitated by polyploidy, hybridization, and stress-induced modification via epigenetic change (Prentis et al. 2008). Vegetative propagation may take advantage of clonal integration to exploit environmental heterogeneity, while apomixis does not restrict the formation of new biotypes which could adapt to heterogeneous ecological conditions.

Clonal integration, i.e., connection among ramets that share water, nutrients, and other substances can improve the plant's utilization of heterogeneous resources thus affecting growth, biomass allocation, photosynthetic performance, etc. and facilitating spatial occupation of new habitats at a local scale (You et al. 2014).

Apomixis, instead, copes more regional scales by using the long distance-dispersal capacities of seeds. Apomictic plants can deal with regional environmental heterogeneity because they are not strictly clonal, they can create new genotypes primarily through residual sexuality and secondly through mutations (e.g., Paun et al. 2006; Hörandl and Paun 2007; but see further details under the section *Apomixis and the formation of agamic complexes*). Because apomixis is mostly facultative, even low levels of functional sexuality are enough to create new genotypic variants and thus facilitate the occupation of heterogeneous environments. In this sense, genotypic variability is higher surrounding the center of distribution of diploid sexual forms or in areas of co-occurrence of diploid sexuals-polyploid apomictics (e.g., Babcock and Stebbins 1938; Daurelio et al. 2004; Cosendai et al. 2013). Moreover, since apomixis is usually connected to polyploidy, and often apomicts are hybrids (Carman 1997), apomictic plants sustain highly heterozygous, vigorous genotypes, which can colonize different environments with, for example, general purpose genotypes (Baker 1965). Therefore, colonization and niche shifts into novel abiotic conditions and environmental heterogeneity could be conducted by genotypes with a high standing intraindividual genetic variation, i.e., intragenomic (allelic) diversity and heterozygosity (Prentis et al. 2008). Additionally, multiple introductions can increase genotypic variability in a newly occupied area (Barrett et al. 2008; Molins et al. 2014) and thus enhance niche space occupancy.

Detection of small-scale genotype–environment interactions is strongly indicative of local adaptation at microsite of a few squares meters and that small-scale environmental heterogeneity is maintaining genetic variation in asexual species (Stratton 1994; McLeod et al. 2012). Polyploidy is another factor that helps asexuals to afford the requirements of diverse ecological niches by, for example,

preserving levels of genetic variability despite the absence of meiotic recombination and genetic segregation.

While even low percentages of genotypic variation could help asexual plants to fulfill ecological demands of heterogeneous environments, the capacity to acclimatize to new conquered microhabitats after exposition to novel abiotic and biotic conditions and to environmentally induced stress seems to be related to epigenetic variation (e.g., DeWalt and Hamrick 2004; Poulin et al. 2005; Hardesty et al. 2012; Roiloa et al. 2014). Such epigenetic fine-tuning would favor the selection of fittest genotypes possible adapted to a variety of microenvironments and the entire occupancy of niche spaces. Experimental work on apomictic clonal dandelions demonstrated immediate response of polyploid apomictic plants to abiotic stress conditions and heritability of epigenetically controlled traits (Verhoeven et al. 2010a, b; Verhoeven and Preite 2013). Asexual plants further change their morphological phenotypes significantly in introduced areas with the same speed as sexual plants (Dalrymple et al. 2015) and show a high ecophysiological plasticity (Molina-Montenegro et al. 2013). Morphological variation in apomictic plants correlated to epigenetic rather than to genetic variation (Rois et al. 2013). Epigenetic markers are in plants at least partially heritable (Verhoeven et al. 2010b) and can be directly influenced by abiotic environments (Bossdorf et al. 2008; Zhang et al. 2013). Other than in animals, the plant germline cells separate late during development in the adult sporophyte, and re-setting of epigenetic methylation does not occur during plant meiosis (Jacobsen and Grossniklaus 2011). Hence, trans-generational inheritance of environmentally induced epigenetic change is present and potentially a powerful mechanism for rapid local adaptation of plants.

Thus, not only genotypic but also epigenetic variations are factors enhancing genotype plasticity and adaptation (e.g., Verhoeven and Preite 2013; Douhovnikoff and Dodd 2015), and hence the capacity of asexual plants to cope better with environmental heterogeneity and niche gradients, promoting the dispersal of fitted genotypes and contributing to the success observed in clonal plants.

16.6 Geographical Distribution and the Dual Effect of Being Asexual: Benefits May also be Constraints

Asexual plants suffer from several restrictions connected mainly to genetic limitations raised by the absence of sex. Because of polyploidy and/or hybridization, levels of genetic variability and heterozygosity may remain similar to those observed in sexual parental species, despite reductions in genotypic diversity (Hörandl and Paun 2007; Beck et al. 2011; Cosendai et al. 2013). Although evolutionary capacities of asexual plants are certainly influenced by such restrictions, still it is not completely clear whether the consequences of mode of reproduction are negative or positive. Natural distribution of sexual–asexual systems offers opportunities to evaluate probably consequences of asexuality in species range

expansion. In some cases, ecological capacities of asexual plants seem to be broader than that of sexual parents as supported by geographical parthenogenesis patterns (i.e., a pattern where sexual diploid and asexual polyploid populations have different distribution areas; Vandell 1928; Bierzychudek 1985; Asker and Jerling 1992; Hörandl et al. 2008), but such assertion has yet not been tested with specific studies. Asexuality had certainly played a crucial role in many cases (e.g., Kearney 2005; Hörandl 2006), whether it is a temporary or lasting role is still uncertain. Range expansion is usually associated with ecological and/or genomic circumstances such as landscape changes, hybridization, or polyploidy, which opens new opportunities for species expansion by releasing new niches and/or creating new combinations of characters that allow the invasion of new habitats (e.g., Babcock and Stebbins 1938; Levin 2000). In some cases morphological and/or genetic differentiation of ecologically divergent lineages may obscure species boundaries and with this researcher's ability to find signs of geographical parthenogenesis patterns since differentiation between sexual and asexual morphotypes will not be possible without a reproductive characterization. Nevertheless, the known cases where asexuality and apomixis were morphologically, embryologically and/or genetically tracked show contrasting patterns of geographic distributions between sexuals and asexuals. Well-known examples such as the *Crepis* complex (Babcock and Stebbins 1938), *Ranunculus kuepferi* (Cosendai and Hörandl 2010), the *Taraxacum* sect. *Ruderalia* complex (Van Dijk 2003), *Paspalum simplex* (Urbani et al. 2002), *Townsendia hookeri* (Thompson and Whitton 2006), and *Crataegus* (Lo et al. 2013) display the classic pattern of geographical parthenogenesis, where sexuals occupy geographically restricted areas usually related to ancient glacial refuges while apomicts exhibit a more extensive occurrence into ecologically more diversified or severe environments. Several non-exclusive hypothesis had been claimed to play a role in establishment of geographical parthenogenesis patterns (reviewed in Hörandl 2009; Vrijenhoek and Parker 2009), some related with reproductive or genetic advantages such as uniparental reproduction (Baker's law, Baker 1955), polyploidy (Comai 2005; Mau et al. 2015), hybridization (Stebbins 1959), and others related to ecological genetic models such as general purpose genotypes (Baker and Stebbins 1965; Lynch 1984) or frozen niche variation (Vrijenhoek 1979, 1984). However, although no single factor might explain geographical parthenogenesis patterns in each particular case, there are many other cases where apomicts do not show a geographically clear asymmetric distribution compared to sexuals, or even they display inverse patterns with narrow distributions and/or occupy less diversified ecological areas. A clear example could be that of the *Boecheira holboellii* complex, diploids (sexual or apomictic) prevailed rather in the northern USA, whereas polyploid apomicts predominate in the southern USA (Dobeš et al. 2004b), with a diffuse geographical pattern between sexuals and apomicts (Sharbel et al. 2005), probably connected to evidence suggesting that diploid apomicts in *Boecheira* are trapped into ecological niches of their parental diploid sexuals (Mau et al. 2015). Another possible case that does not show the typical pattern of geographical parthenogenesis would be that of *Bouteloua curtipendula* Michx., where apomicts are restricted to semi-arid regions from

southwestern USA and northeastern Mexico while sexual forms occurs from central and eastern USA till central Mexico (Gould 1959).

Patterns of geographical distribution depend also upon specific biogeographical history of an apomictic group (Hörandl 2006), whenever a complex biogeographical scenario of, for example, past fragmentation, recolonization, isolation-by-distance, and glacial refuges have certainly shaped geographical range of sexual and asexual biotypes (e.g., Dobeš et al. 2004a, b). As mentioned by Hojsgaard et al. (2014b), it became clear that geographical parthenogenesis is an opportunistic strategy that is not necessarily realized by every agamic complex.

The overall observed geographic patterns of sexual–asexual plant systems suggest that either (1) it is an effect of the evolutionary stage of the agamic complex and then smaller distributions of asexuals is related to the age (too young or too old) of the agamic complex rather than to a disadvantage of asexuality; or (2) the consequences of apomixis, or features associated with, are sensed differentially by diverse plant systems and hence have a dual effect, in some cases potentiating while in others restraining species ecological capacities to foster range expansion.

Accordingly, the impact of parthenogenesis on plant ecological capacities may depend upon other particularities related more to specific features of the taxon, such as physiological (phenotypic) plasticity, intragenomic (allelic) diversity and heterozygosity, little tolerance to genome doubling, among others that could constrict plant ecological capacity to recognize and access open or free niches. Thus, if a plant cannot fulfill requirements for niche occupancy, the mentioned theoretical advantages of apomixis will turn into ecologically trivial, fallow features. A graph representing plant ecological capacity or plasticity to fulfill requirements (or not) and hence colonize an open niche and take advantage of apomixis to expand species distribution is presented (Fig. 16.4). The degree of stabilization and penetrance of apomixis after emergence would also influence the plant's capacity to explore new habitats and increase range distributions when clonal genotypes with narrow niche breadth are tightly fitted to, and occupy a new patch, since high levels of sexuality may break up the fittest genotype and create new “sub-adapted” gene combinations no coping with niche requirements of consecutive patches. In spite of this, certain level of sex would be crucial to facilitate the conquest of new niches exposed to the facultative apomictic lineages during range expansion.

16.7 A Returning to Sex Can Fuel Ecological Genetic Divergence and Diversification

Clonal propagation fosters the expansion of certain genotypes at the micro-geographic scale. Depending on the type of clonal propagation, range distributions can vary, as runners expand easily and faster than rhizomes. However, clonal propagation at local geographical scales has the disadvantage that once a flowering period is activated (whether by ecological and/or environmental factors), gene flow between diverse clonal ramets would create new recombinant genets, uniformize the

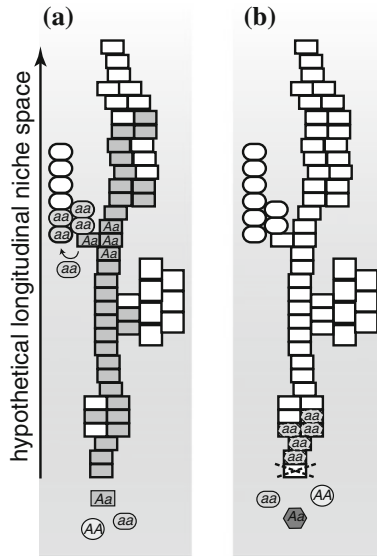


Fig. 16.4 Scheme representing a hypothetical niche offered to two species with different ecological plasticities and capacities to fulfill niche requirements. Because of particular genetic, epigenetic and ecophysiological features, species in (a), can fulfill the niche requirements (*rectangles*) and occupy the niche space (*colored rectangles*) by multiplying apomictically the same genotype while propagating into consecutive patches and thus accessing moderately different niches (*squares* or *ovals*). Facultative sexuality or other processes generating variation in clonal progenies (e.g., mutations or epigenetic changes; see details in the text) could facilitate the formation of genotypes with novel ecological capacities to access new open niches and occupy them by taking advantages of asexual reproduction. Contrary, species (b), has a genetic background and ecophysiological features that not allow filling niche requirements (no “rectangle” genotypes), although sub-adapted genotypes (“oval” genotypes) may access some patches. In such cases, only a fine-tuning toward a fitted genotype might allow the exploitation of apomixis advantages to expand species distribution range and/or access other connected niches.

gene pool and generate a net of closely connected individuals with restricted chances of further diversification and differentiation. Even if single clonally propagated genets are locally restricted in subpopulations, selection and divergence of genets adapted to particular microenvironments will be limited by regular flowering (i.e., relative rate of sexuality), reducing pair-wise allelic divergence and hence coalescence times (Austerlitz et al. 1997; Bengtsson 2003). The extent of such process would depend on the extent of the range expansion (i.e., geographic sub-divisions) and the time to the last flowering period (sexuality rate), and nonetheless will certainly shape patterns of genetic and genotypic variation within populations.

Apomictic plants, on the contrary, disperse clonal seeds and reach more regional geographic scales. In this case, not only genotypic but also epigenetic variation are factors enhancing the capacity of asexual plants to cope better with environmental heterogeneity and niche gradients, promoting the spreading of fitted genotypes. Such range expansion occurs first at local and then at regional geographical scales

and generate a mesh of relatively restricted gene flow among apomictic individuals within and among populations that will work as a dense sieve, slowing down or even interrupting genetic cohesion and isolating *ipso facto* populations located at distances that, in a sexual species, rates of gene flow are allowed and expected. The absence of the genetic cohesiveness granted by sexuality is a major consequence of apomixis in plants, which creates independent lineages, genetically isolated, and promotes faster genetic divergence among them (e.g., Bengtsson 2003) by changes other than recombination and genomic resetting of meiosis. Therefore, changes which usually had limited influence on sexual reproducing populations (e.g., mutations and epigenetic signals) had magnified effects among asexual non-recombinant asexual individuals. Consequently, sexuals show regional gene pools, whereas apomicts had several unique gene pools (e.g., Paun et al. 2006; Cosendai et al. 2013; Molins et al. 2013).

This is in agreement with observations that indicate that the higher is the distance to the sexual parental populations, the higher the degree of clonality and the less the genotypic diversity, so that remote areas are dominated by genotypes selected by the harshness of the environment (e.g., Babcock and Stebbins 1938; Daurelio et al. 2004). On the other hand, the farther away the distance of the founder event from the diversity center (sexual parental populations), the less probable to be reached by any migrants, and hence the less genotypically variable will be the population (depending too of the degree of residual sexuality present). Since reproductive shifts can be expected to occur in both directions (Hörandl and Hojsgaard 2012), a return to sexuality in any of the apomictic widespread lineages would found a new, geographically and genetically isolated population with a definite divergent fate. In remote areas, the pressure for a reversal to sexuality—whether realized or not—would probably be higher whenever the clonal genotype cannot adapt to or fulfill environmental requirements. Yet, reversals to sex are so far rough of examination. A few cases have been documented as likely reversions from apomictic to sexually (near) obligated reproduction in plants (see Hörandl and Hojsgaard 2012). Reasons can be diverse. Primarily, once a new sexual population is established, it can be hard to distinguish whether its evolutionary source is from an agamospermous lineage or from a sexual putative parental species. Secondly, because of constraints to the establishment of a sexual population (see next section), new sexual individuals may have a short-lived existence. Nevertheless, once established and mainly due to the facts mentioned above, the new sexual population will undergo genetic isolation that will drive it into an independent evolutionary path. Even though a complete block of the gene flow is not apparent in most of apomictic complexes studied (e.g., Hörandl et al. 2009; Cosendai and Hörandl 2010), the present levels of sexuality at the micro-geographic scale crack gene pools and can work as a very efficient “isolation net” at the macro-geographic scale. Whether limiting or interrupting gene flow among geographically related or distant apomictic clones, the only chance of genetic interchange between the neo-sexual and any other sexual population would be subject to migrants and hence, to the distance to the former sexual parental populations/species and the specific dispersal abilities of the species. Thus, the farther away the neo-sexual population is found, the less

probable to be reached by any migrants from sexual parental species, and the most likely to have divergent, distantly located, sexual populations.

The lifespan and destiny of both the new seeded and the original sexual populations would depend upon diverse factors, but if lasting, will certainly have a robust evolutionary potential for speciation and further diversification. This model is supported by the observation that occurrence of apomixis in angiosperms is highly correlated to clades with higher levels of diversity (i.e., higher genera and/or species numbers) (Hojsgaard et al. 2014a), reinforcing the hypothesis that apomictic pioneer plants often promote range expansion and enhances plant diversification by founding neo-sexual isolated populations.

16.8 Challenges of the Neo-Sexual Populations

Most striking challenges of reverted sexual individuals that will have a strong influence on plant population dynamics are related to Allee-effects, i.e. negative effects of low population density or small population size on mean individual fitness (Courchamp et al. 2008). Many mechanisms are known to cause an Allee-effect. The best-documented mechanism for plant species is pollination limitation (e.g. Groom 1998; Davis et al. 2004; Xia et al. 2013a), but also predation, breeding system, reproductive facilitation, interspecific reproductive interference, inbreeding depression can lead to an Allee-effect (e.g. Fischer et al. 2000; Wagenius et al. 2007; Xia et al. 2013b). Since (polyploid) apomictic taxa do not undergo recombination during the reproduction process, they are not strongly affected by inbreeding consequences and maintain high levels of heterozygosity (Hörändl 2006). Conversely, self-compatible sexual species may display high levels of homozygosity due to founder effects following introduction into a new niche and therefore experience severe losses of genetic diversity and heterozygosity (e.g., Lynch 1984). Thus, a few reverted sexual individuals will suffer the same genetic consequences that will constrain the establishing of reproductively stabilized sexual individuals

Additionally, because apomictic plants produce seed embryos without fertilization, and consequently, sexual individuals cannot fertilize apomictic ones, a reversal to sex may have an ephemeral existence if unidirectional introgression of apomixis is not avoided before the establishment of a statistically representative number of reverted individuals. Usually, although few examples of interploid gene flow are known in the wild (e.g., Chapman and Abbott 2010; Pinheiro et al. 2010), differences in ploidy sets represent a relatively efficient barrier to character introgression, including complex features such as apomixis into sexual species (e.g., Hörändl and Tensch 2009). However, in the case of a new sexual population derived from an agamosperous lineage, ploidies will be equal and hence without a niche shift or any disadvantage discouraging the coexistence of the neo-sexual and the putative parental apomictic lineages, the establishment phase for a new sexual population will be highly vulnerable.

Another major disadvantage to the new sexual individuals could be related to pollinator limitation, as they would be surrounded by apomictic plants and hence not available for pollen transfer between sexual (self- or outcrosser) plants. Self-compatibility or shifts in phenology could overcome this minority (reproductive) cytotype disadvantage.

Finally, the re-establishment of sexuality could stimulate the access to new niches, mainly at the borders of apomictic distributions where genetic and epigenetic limitations would not allow further expansion. Thus, the success of the neo-sexual individuals would be mainly related to their relative capacity to become ecologically differentiated and conquer new niches for which the apomicts are not adapted and/or some genetic restrictions limit them to access such habitats.

Once a reversal is successfully established, a genetically cohesive gene pool canalized through high levels of gene flow would strengthen the isolation from surrounding asexual plants and facilitate the divergence of the new population from the original one(s).

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